A CYTOLOGICAL AND GENETICAL STUDY OF TRIPLOID MAIZE

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INTRODUCTION

During the course of investigation on the chromosome number and behavior of different genetic strains of maize a triploid individual appeared in an otherwise diploid culture. As has been reported in a preliminary note (RANDOLPH and MCCLINTOCK 1926), this individual was notably more vigorous than its diploid sibs. Since the triploid possessed certain known genetic characters it was desired to follow the genetics along with the cytology in the descendants of this individual.

In the preliminary note it was suggested that the triploid probably arose through the fusion of a diploid and a haploid gamete. Since the publication of this note much evidence has accumulated which would support this probability (see pp. 209 and 209; see also figures 17 and 27).

The literature on Zea chromosomes is rapidly becoming more extensive. Since Miss FISK (1927) has reviewed most of the existing literature on the subject (KUWADA 1911, 1915, 1919, 1925; LONGLEY 1924, 1925; FISK 1925; KIESSELBACH and PETERSEN 1925) little more need be said with regard to

previous investigations on Zea. To this list we might add the short paper of REEVES 1925, in which it is stated that of 8 varieties of maize examined, 7 showed 10 pairs of chromosomes during meiosis; the eighth, a Black Mexican variety, on the other hand, showed 12 pairs. LONGLEY (1927) and RANDOLPH (1928) in recent investigations have extended considerably our knowledge of the behavior during meiosis and the distribution through gametes of such "extra" chromosomes.

It is possibly unjust to restrict the term triploid to those 3n forms which show trivalents during meiosis. However, in the 3n Zea plants showing 10 trivalents, behavior during meiosis can be compared directly with other 3n forms which show trivalents. The literature on such types is growing rapidly. Under the heading of triploids showing trivalents would come some individuals of Morus (OSAWA 1920), Canna (BELLING 1921, 1925), Datura (BELLING et al.), Hemerocallis (BELLING 1925), Hyacinthus (BELLING 1925), Campanula (GAIRDNER 1926), Lycopersicum (MANN-LESLEY 1926) Zeax Euchlaena F_1 (LONGLEY 1924; Randolph unpublished), Drosophila (METZ 1925; MORGAN 1925; BRIDGES 1921, 1922, 1925) and Zea.

The genetics of triploids has been followed in the case of Datura, Drosophila and Lycopersicum. For the literature on trisomic inheritance, see discussion under Genetic Investigation.

MATERIAL AND METHODS

The behavior of chromosomes during meiosis, exclusive of the early prophase stages, has been studied in many diploids, two triploids and 50 F_1 individuals resulting from direct and reciprocal crosses made between diploid individuals and the triploid plant (see table 1). Studies were made only on microsporcytes.

For the study of chromosome number and behavior during meiosis the iron-aceto-carmine method was found to be very serviceable. In some cases the smears were dried slowly and then mounted in balsam. Photomicrographs 14 and 15, in plate 6 and text figure 7 were made from preparations seven months old which had been so treated. In some cases where the stain was too heavy it was extracted in a weak solution of acetic acid, the whole slide being warmed to hasten the extraction.

Other sporocyte material and root tips were fixed in a Bouin solution modified according to Allen, mounted in paraffin and sectioned 10-15 microns thick. Heidenhains iron-alum-haematoxylin and Flemming's triple stain were used.

The photomicrographs were taken with the aid of a Leitz "Makam" camera, an 8× periplanatic ocular, and a 1.8mm, N.A.1.25 Spencer achromatic objective. A Wratten green filter, number 56, was used to increase definition.

A BRIEF RÉSUMÉ OF MEIOTIC BEHAVIOR IN DIPLOID INDIVIDUALS

At diakinesis the diploid individuals show characteristically 10 pairs of chromosomes. At the time the nuclear membrane disappears the bivalent nature of the chromosomes becomes relatively indistinct because the chromosomes are so contracted and closely appressed. However, after the bivalent chromosomes line up at the equator and show evidence of commencing anaphasic disjunction, characteristic forms are assumed (see bivalent chromosomes in metaphase figures in plates 2-5).

The double (dyad) nature of each chromosome of the pair is clearly indicated at early anaphase, frequently before the chromosomes have completely disjoined. It is evident from a study of metaphase *I*[1], early anaphase *I*, and metaphase *II* that the spindle fiber attachment is either sub-terminal, sub-median or median.

In consequence of partial anaphasic separation of members of the dyads the chromosomes appear as double Vs (median or sub-median attachments, or as almost single Vs (sub-terminal attachments). This picture varies considerably in different anaphases due to the unusual compactness of the dyads in some figures and to their loose, long-armed form in other figures (figure 34). In the latter case one or more arms of a dyad may become much pulled out, remaining near the equator during the continued poleward advance of the spindle attachment part of the chromosome. The telophase passes over into a more or less typical interphase wherein the individual chromosomes lose their observable identity. A cell plate, apparently initiated by the phragmoplast, is evident at this time.

From the very earliest prophase of *II* in which the chromosomes can be recognized as distinct bodies, their form is very characteristically that of an H or an X. Contraction of the chromatic material continues until the chromosomes become relatively small Hs and Xs (figure 31). The nuclear membrane shrinks about the chromosomes with the formation of a multipolar spindle. This, in turn, passes into a bipolar spindle with the disappearance of the nuclear membrane. The shape of the metaphase *II* chromosomes depends greatly upon the amount of contraction of the chromosomes at this time. In some cases the dyads appear as relatively long, double threads. On the other hand, if contraction of the chromosomes

[1] The first meiotic mitosis will be designated as *I*, the second meiotic mitosis as *II*.

continues, many of these dyads appear as double 'dumb-bells", the dumb-bell shape probably being due to an accentuated constriction (see SAKAMURA 1920; GOTOH 1924). Apparently the anaphase *II* chromosomes derive their varied shapes, such as bent rods in some sporocytes, or dumb-bell-like bodies in others, from the state of contraction of the chromosomes at metaphase *II*. As a result of division *II* a quartet of spores is formed. Cell plate formation apparently initiates wall formation as has been shown by REEVES (1928).

In most cases meiosis is thus characteristically regular, but several types of behavior having much theoretical interest have been observed. Occasionally and sometimes rather frequently in certain diploid cultures a pair of chromosomes showed non-conjugation as described by BELLING (1925) and others. Many of the diakinesis figures within an anther contained distinctly 10 bivalent chromosomes, while other sporocytes within the same anther showed $9^{II}+2^{I}$.[2] Whether there was never any meiotic association of the 2 homologous chromosomes or whether the disassociation of a synapsed pair to form 2 univalents took place in late prophase *I* is unknown. Neither is it known whether the same homologous pair was concerned each time a figure with $9^{II}+2^{I}$ was observed. The cause of this appearance is certainly not a lack of homology of the chromosomes in all cases (RANDOLPH 1928).

Other irregularities such as non-disjunction of a pair of chromosomes, lagging and splitting of univalents at *I*, two-nucleated sporocytes, metaphase *I* figures with more or less than the expected chromosome number, and metaphases and anaphases with multiples of the diploid chromosome number have been observed in diploid individuals.

MEIOSIS IN THE TRIPLOID INDIVIDUAL

A brief description of meiosis in a triploid plant has been given (RANDOLPH and MCCLINTOCK 1926); therefore certain features stressed in that paper will not be redescribed here.

Diakinesis stages in aceto-carmine in the triploid gave far better results than similar stages in fixed and sectioned material. In the former method the synaptic condition, that is, whether trivalent, bivalent, or univalent, of all the chromosomes in a single nucleus usually could be determined (figure 1),[3] whereas, in the section only a few of the chromosomes within

[2] Bivalents will be designated by the exponent Roman numeral II; univalents, exponent I; trivalents, exponent III, etc.

[3] Figures in plates 1–5 are numbered from 1–47. The photo-micrographs in plate 6 are numbered 1–15. To avoid confusion, "plate 6" will always be added to the figure number when reference is being made to the photo-micrographs.

EXPLANATION OF PLATES

Figures in plates 1–5 were made with the aid of an Abbe camera lucida. Approximate magnifications:

Figures 1–24, 26–29, 32–46: 1200x.

Figures 25, 30, 31: 500x.

Figure 47: 700x.

Figures in plates 1 and 6 are from aceto-carmine smears and sectioned material. Figures in plates 2–5 from aceto-carmine smears only. The small numbers at left of figures indicate the culture and plant number.

PLATE 1.

FIGURE 1.—Diakinesis in microsporocyte of triploid (56_2), showing 10 trivalents. Aceto-carmine.

FIGURE 2.—Diakinesis in triploid, showing 9 trivalents, 1 bivalent and 1 univalent. Sectioned material.

FIGURE 3.—Metaphase *I* in triploid, showing 10 trivalents. Aceto-carmine.

FIGURE 4.—Metaphase *I* in triploid. 10 trivalents. Sectioned material.

FIGURE 5.—Metaphase *I* in triploid. 9 trivalents, 1 bivalent and 1 univalent; univalent preparing to split and separate while trivalents and bivalents disjoin. Sectioned material.

FIGURE 6.—Metaphase *I* in triploid. 7 trivalents, 3 bivalents and 3 univalents. 2 univalents in the spindle region nearer the lower pole, 1 in the cytoplasm outside the spindle. Sectioned material.

FIGURE 7.—Metaphase *I* in triploid. 8 trivalents, 1 bivalent and 1 univalent in main spindle; 1 trivalent in separate spindle running perpendicular to plane of section. See photograph of same: plate 6, figure 5.

FIGURE 8.—Anaphase *I* in triploid. 15 chromosomes going to each pole. Aceto-carmine.

FIGURE 9.—Anaphase *I* in triploid. 14 dyads at each pole; 2 lagging and separating in center of figure. Sectioned material.

FIGURE 10.—Anaphase *I* in triploid. 12 dyads in upper pole, 11 in lower pole and 7 separating dyads in center of spindle. See photograph of same plate 6, figure 6. Sectioned material.

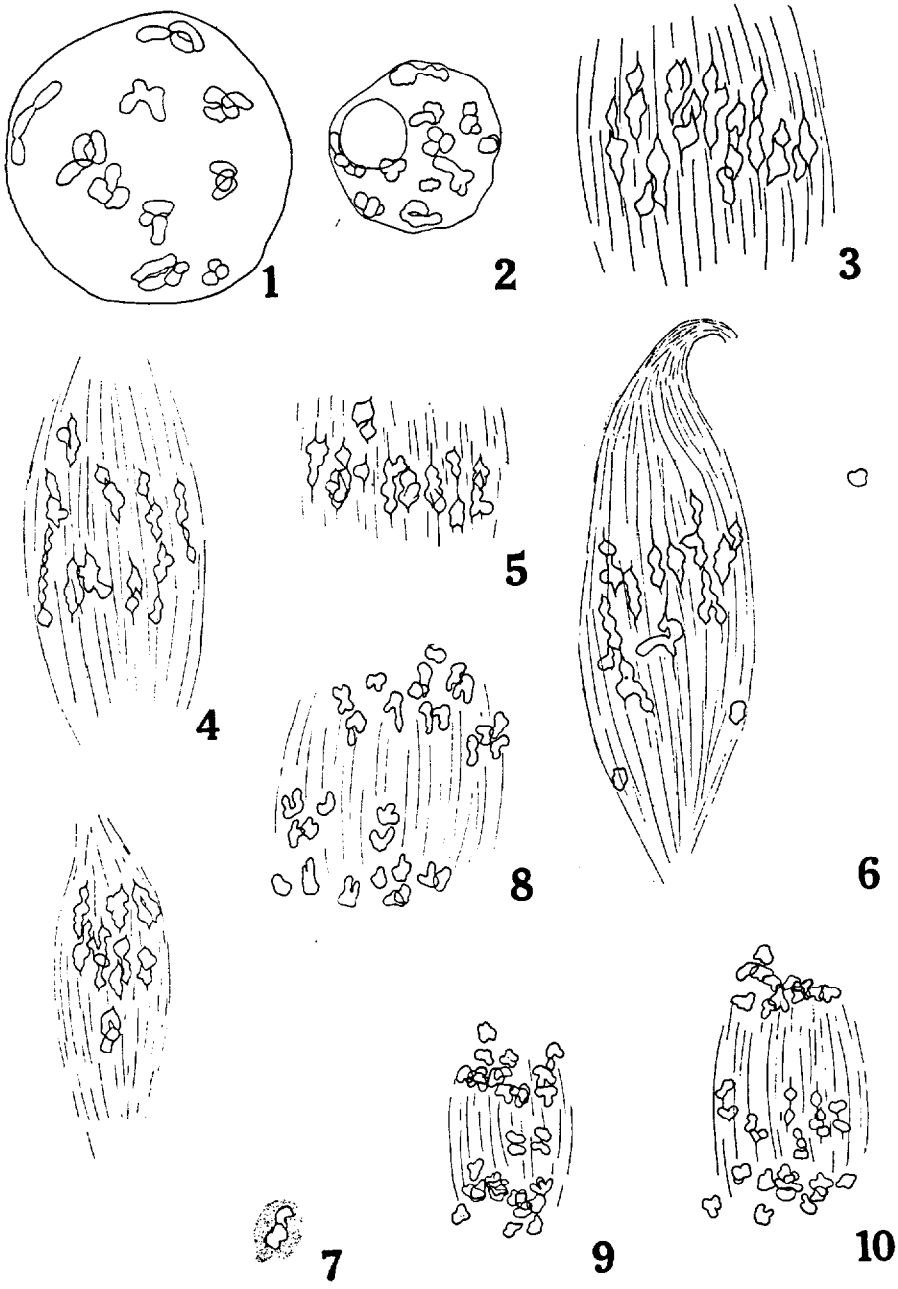
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PLATE 2

Figures from 2n+1 F_1 plants.

FIGURE 11.—Metaphase *I* showing $9^{II}+1^{III}$.

FIGURE 12.—Metaphase *I* from same plant showing $10^{II}+1^{I}$. The univalent is lying in the equatorial plate.

FIGURE 13.—Same as figure 12, only the univalent is lying toward the upper pole.

FIGURE 14, 15, and 16.—Metaphase *I* trivalents taken from different $9^{II}+1^{III}$ figures arranged to show the various appearances of the same trivalent in different cells and the trivalents from different 2n+1 plants.

FIGURE 17.—Metaphase *I* in a 2n+1 plant, showing the double number of chromosomes ($20^{II}+2^{I}$) in one figure.

FIGURE 18.—Metaphase *I* spindle with four times the normal number of chromosomes: $40^{II}+4^{I}$.

FIGURE 19.—Three connecting metasphase *I* spindles in a plasmodial mass.

FIGURE 20.—Anaphase *I* figure in a 2n+1 plant, showing fragmentation of chromosomes in progress.

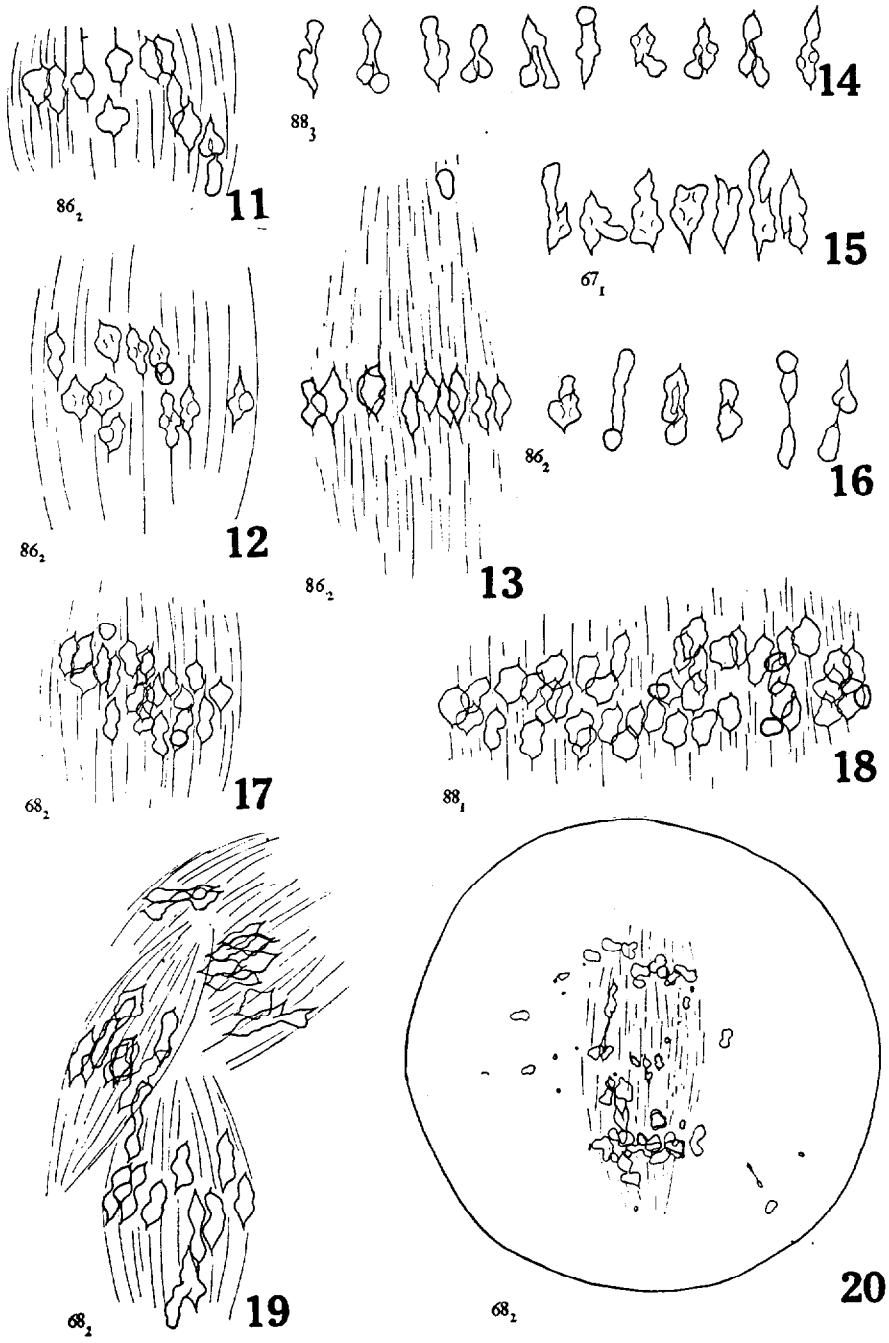
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PLATE 3

Figures from 2n+2 F_1 plants.

FIGURE 21.—Diakinesis: $9^{II}+1^{III}+1^{I}$.

FIGURE 22.—Late metaphase *I*: $8^{II}+2^{III}$. The members of the trivalent to the right have nearly disjoined.

FIGURE 23.—Metaphase *I*: $10^{II}+2^{I}$.

FIGURE 24.—Anaphase *I*: 10 dyads in upper pole, 11 toward lower pole, 1 dyad with separating halves at center of spindle.

FIGURE 25.—Microspore quartet with unequal spores.

FIGURE 26.—Metaphase *I*: $7^{II}+2^{III}$. This figure contains 1 bivalent less than most of the sporocytes in this plant.

FIGURE 27.—Metaphase *I*: $4^{II}+6^{IV}+2^{VI}$. 2 large sexivalents above and below plate region; counting from the right in region of plate, the second, third, fourth, sixth, seventh and eighth. groups are quadrivalents, the remaining 4 chromosomes are bivalents.

FIGURE 28.—Anaphase *I* in same plant with the double number of chromosomes.

FIGURE 29.—Anaphase *II*: 12 monads at each pole.

FIGURE 30.—Microspore quartet resulting from *I* and *II*. Note chromatic bodies in cell plate region.

FIGURE 31.—Prophase *II*: 10 dyads in cell to left, 12 dyads in cell to right.

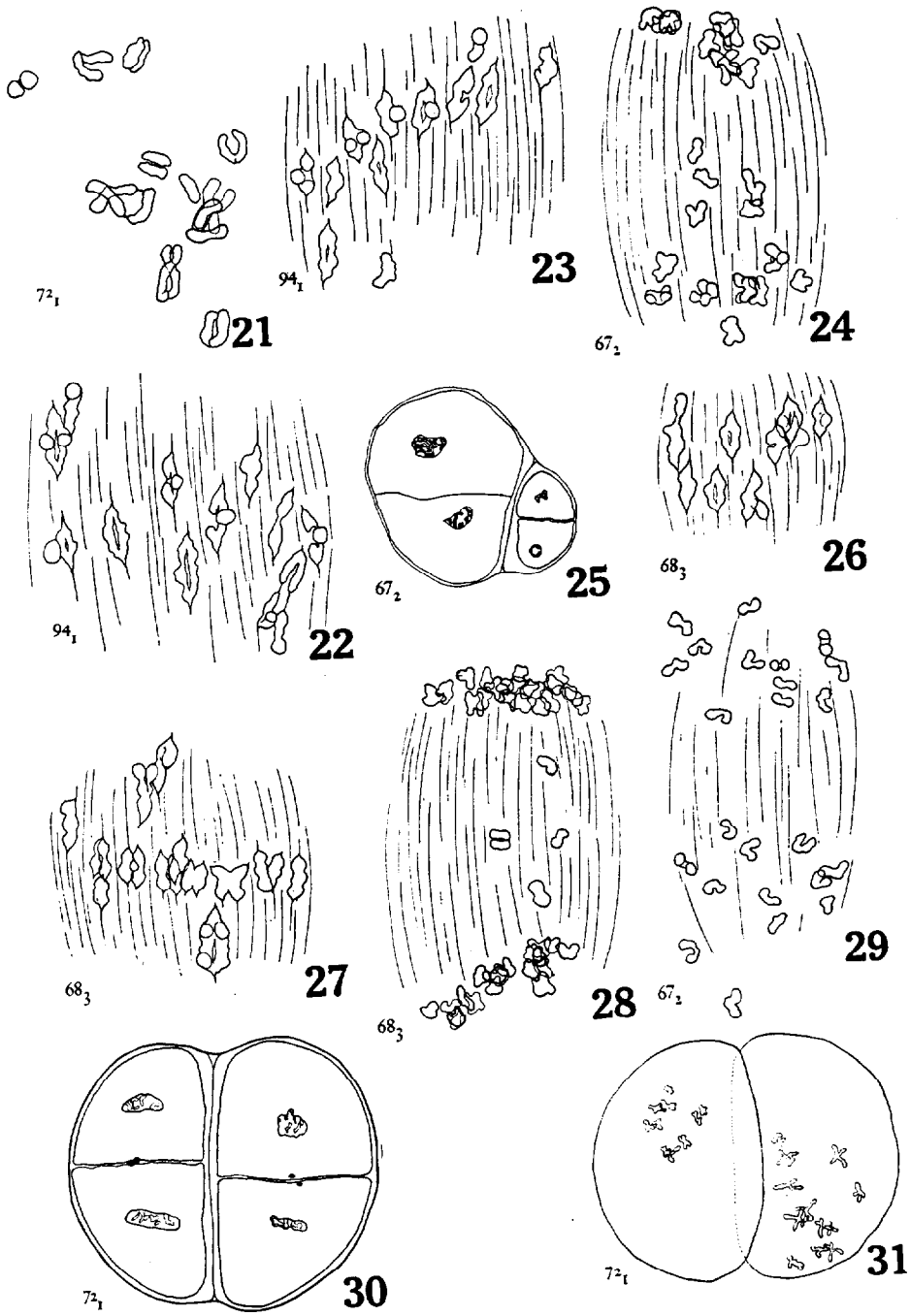
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PLATE 4

Figures from 2n+3 to 3n F_1 individuals.

FIGURE 32.—Metaphase *I*: $7^{II}+3^{III}$.

FIGURES 33.—Metaphase *I*: $8^{II}+2^{III}+1^{I}$.

FIGURE 34.—Anaphase *I* in 2n+3 individual: 10 dyads toward upper pole, 11 towards lower pole, 2 splitting at center of spindle.

FIGURE 35.—Metaphase *I*: $6^{II}+4^{III}$.

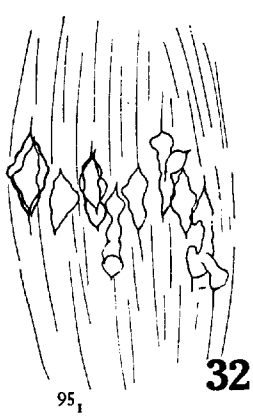
FIGURE 36.—Metaphase *I*: $8^{II}+1^{III}+4^{I}$.

FIGURE 37.—Metaphase *I*: $6^{II}+4^{III}$. See photograph of same, figure 14, plate 6.

FIGURE 38.—Metaphase *I*: $3^{II}+7^{III}$. Members about to disjoin in 2 trivalents at left of figure.

FIGURE 39.—Metaphase *I*: $6^{II}+4^{III}$.

FIGURE 40.—Metaphase *I*: 10^{III}.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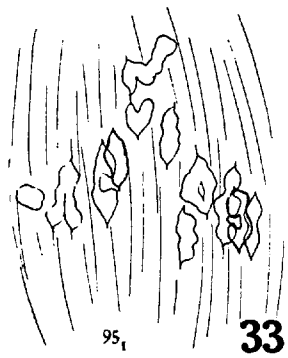
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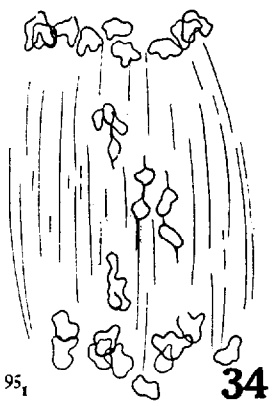
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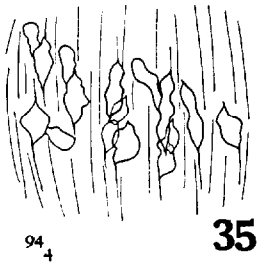
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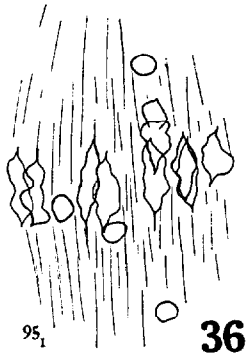
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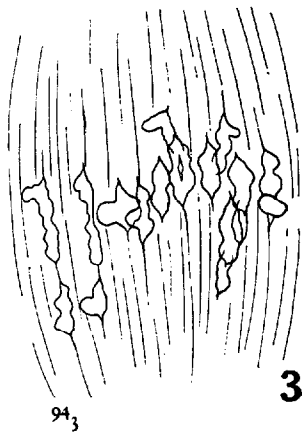
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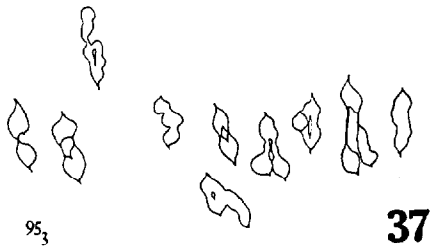
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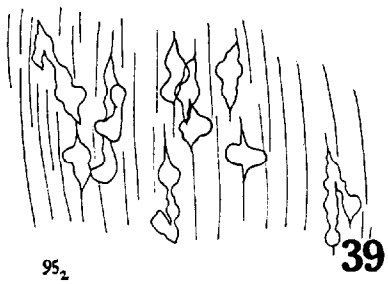
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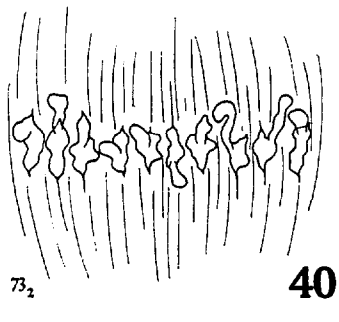
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PLATE 5

All figures are from plant 94_2, 2n+5.

FIGURE 41.—Metaphase *I*: $5^{II}+5^{III}$.

FIGURE 42.—Metaphase *I*: $9^{II}+7^{I}$.

FIGURE 43.—Diakinesis: $4^{II}+3^{III}+8^{I}$.

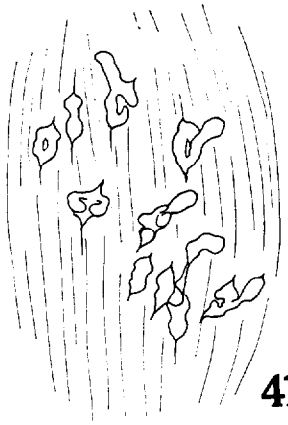
FIGURE 44.—Division *I*: 25^{I}.

FIGURE 45.—Anaphase *I*: 10 univalents at upper pole; 11 at lower pole; $1^{II}+2^{I}$ at center of spindle.

FIGURE 46.—Early anaphase *I*: $1^{II}+1^{III}+20^{I}$.

FIGURE 47.—Showing production of 6 unequal spores from a single microsporocyte.

McCLINTOCK, B., TRIPLOID MAIZE



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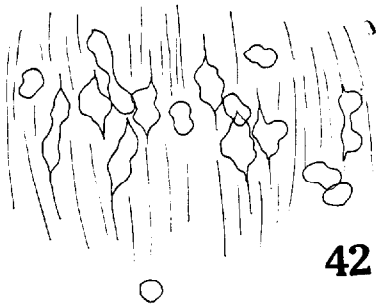

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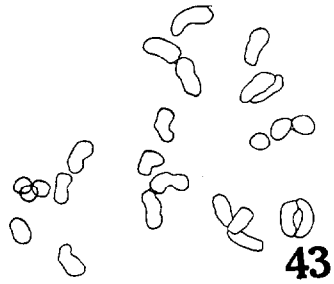

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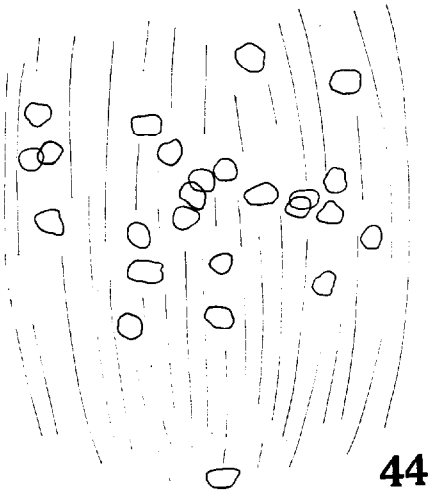

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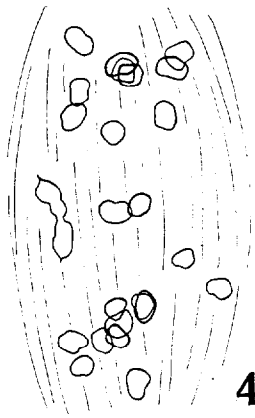

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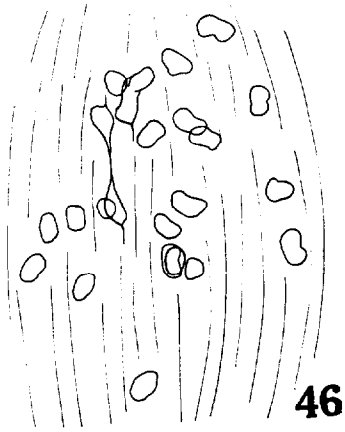

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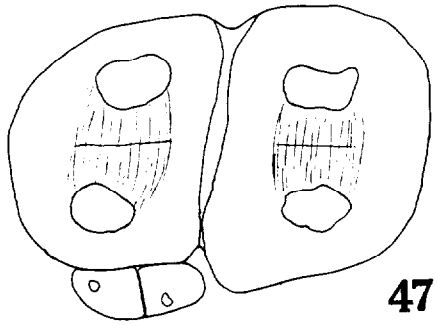

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PLATE 6

Figures 1–13 are of sectioned and haematoxylin stained material. Figures 14 and 15 are of ceto-carmine smears. Magnification, approximately 680x.

FIGURE 1.—Diakinesis in triploid (56_2). One trivalent visible.

FIGURE 2.—Late metaphase *I* in triploid showing disjunction of 3 members of a trivalent.

FIGURE 3.—Same sporocyte as in figure 2, showing another trivalent.

FIGURE 4.—Metaphase *I* in sporocyte of triploid, showing 3 trivalents in same focus.

FIGURE 5.—Metaphase *I* with 2 spindles. Small spindle to right of cell runs perpendicular to the plane of the section and contains one trivalent. See drawing of same in plate 1, figure 7.

FIGURE 6.—Anaphase *I* showing lagging and separation of halves of split univalents. Same as figure 10, plate 1.

FIGURE 7.—Prophase *II* in triploid. Spindles are forming about both dwarf and major nuclei.

FIGURE 8.—Telophase of *I*; two large cells and one small cell. The nuclei of the two large cells are not in focus.

FIGURE 9.—Telophase of *II* resulting from a tripolar spindle.

FIGURE 10.—Formation of "dwarf" nuclei from prophase *I* nucleus. Arrow 1 points to 3 small nuclei in row. Arrow 2 points to a larger nucleus beside major nucleus.

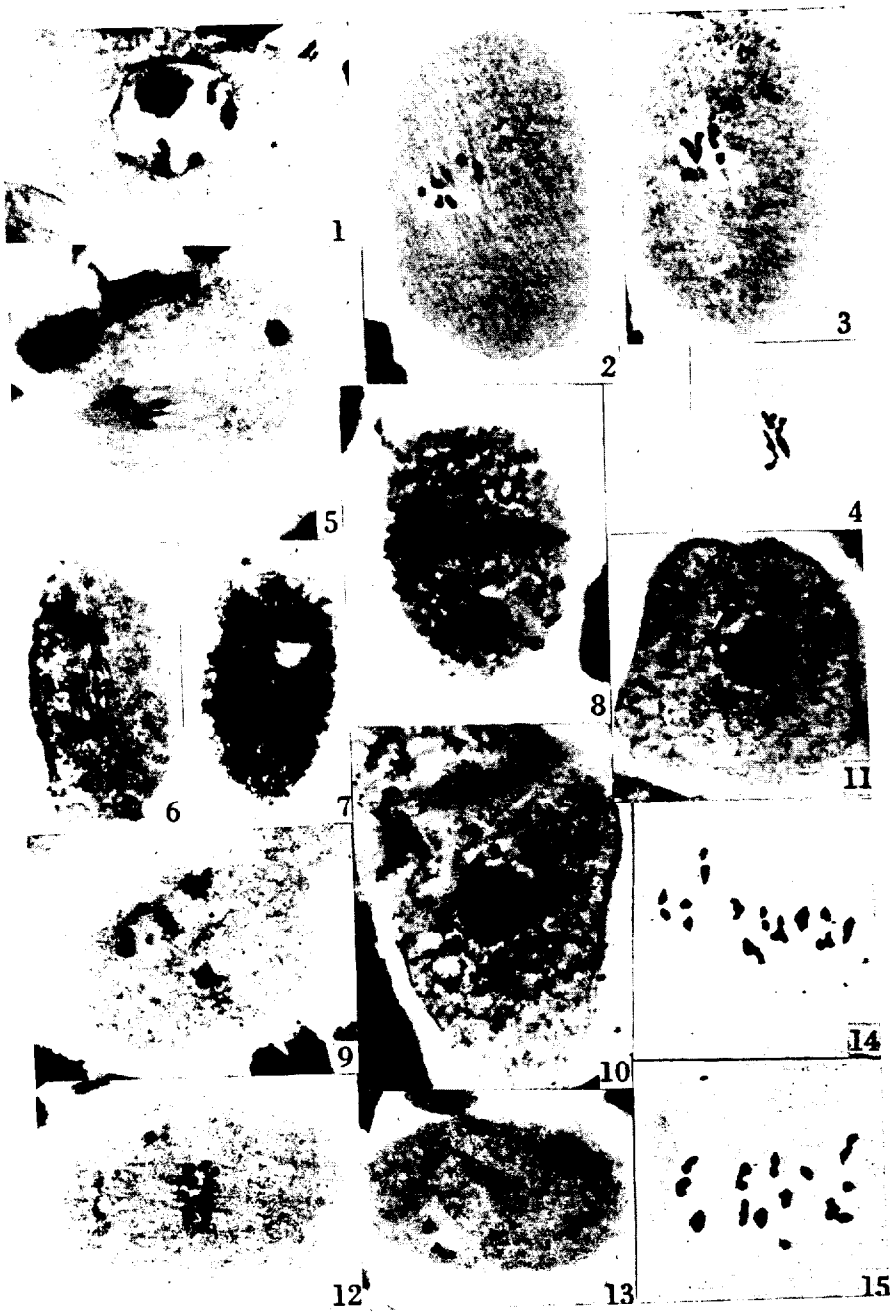
FIGURE 11.—Prophase *I*. A chromatic thread apparently projecting through the nuclear membrane into the cytoplasm.

FIGURE 12.—Early anaphase *II* in triploid. Sporocyte possessing but one spindle containing the double number of chromosomes.

FIGURE 13.—Metaphase *II* in triploid showing several spindles, variously oriented, with few chromosomes in each.

FIGURE 14.—Metaphase *I* in 2n+4 individual (95_3) showing $6^{II}+4^{III}$. Same as figure 37, plate 4.

FIGURE 15.—Metaphase *I* in adjacent sporocyte to above showing $10^{II}+4^{I}$.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a nucleus could be easily interpreted as a general rule. Occasionally all the chromosomes in a single nucleus could be well interpreted (figure 2, plate 1; figure 1, plate 6).

In many cases the chromosomes at diakinesis are arranged in ten groups of three each (figure 1). A definite and typical association of any 3 homologues, giving a constant, morphologically recognizable trivalent, apparently does not exist. This is more clearly evident in F_1 individuals in which the single extra chromosome forms one trivalent, the different figures of which are directly comparable (see plate 2, figures 14, 15 and 16). We see here that the same trivalent both in diakinesis and metaphase *I* assumes various forms which are undoubtedly due to the relative closeness and type of approximation of the three members.

Figure 2 illustrates an apparent tendency on the part of one of the homologous chromosomes to disassociate from the other two. In diakinesis all stages of approximation of the third chromosome are seen: a group of three equally spaced chromosomes; a group which would definitely be recognized as a bivalent with an attached univalent; a bivalent with the univalent rather distantly attached by a fine thread; and finally, an apparently complete disassociation of the univalent from the bivalent. It is obvious, therefore, that although distinct univalents are evident at diakinesis, this by no means indicates that synapsis among the three homologues had not taken place at an earlier prophase stage.

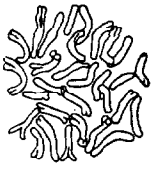

FIGURE 1.—Polar view of somatic metaphase from root tip of triploid plant. 3n=30.

As has been stated, the proportion of trivalents, bivalents and univalents varies in adjacent sporocytes. The presence of 9 trivalents, 1 bivalent and 1 univalent was most usual, those with 2, 3 and 4 univalents being less frequent. We observed in no case more than 4 univalents, that is, $6^{III}+4^{II}+4^{I}$. It is not at all inconceivable, from what is known of the F_1 individuals, that greater disassociation took place but was unobserved in the material examined.

Again, at metaphase *I* we find, very frequently, 10^{III}(figures 3 and 4). However, as in diakinesis, there are commonly present fewer trivalents with a consequent increase in bivalents and univalents (figures 5 and 6).

Sometimes no equatorial plate was formed, the metaphase *I* chromosomes being distributed along the length of the spindle (figures 4 and 6).

In position and behavior the univalents vary considerably. Sometimes they appear in or near the plate. Here they are easily distinguishable because of their smooth contour and their round or oblong shape. However, very occasionally, a univalent lying in the plate exhibits distinct spindle fiber attachments (figure 5). Here the univalent is probably preparing to divide at the same time that the trivalents and bivalents are about to disjoin. This is in contrast to the usual appearance of the separation of the members of a dyad in *I* which takes place in lagging chromosomes after disjunction of the members of the trivalents and bivalents. Sometimes the univalents lie within the spindle area some distance from the plate on either side.

It is not uncommon to find one or more univalents lying in the cytoplasm apart from the spindle (figure 6). Occasionally a sporocyte was observed with one trivalent lying in a separate spindle distinctly apart from the main metaphase *I* spindle (figure 7, and photograph of same, plate 6, figure 5). In other sporocytes the minor spindle was connected with the major spindle.

The distribution of the chromosomes in anaphase *I* appears to be a random one. In many anaphase *I* figures the chromosomes passed to the poles without irregularities (figure 8). However, in many other figures marked irregularities were obvious, such as lagging of dyads, lagging and splitting of dyads (figures 9, 10; figure 6, plate 6) and splitting and partial separation of a dyad which had commenced to pass to one pole. Other irregularities, such as the fragmentation of part of a dyad as it passed to the pole, were numerous in some sporocytes of certain anthers. The extent of fragmentation within a sporocyte varied from a part of a single dyad to practically the whole complement.

In consequence of the many irregularities observed in diakinesis, metaphase *I* and anaphase *I*, the appearance of the sporocytes in telophase and interkinesis is diverse. In some we find two nuclei of approximately equal size between which a cell plate has formed. In figure 8, plate 6 is shown the formation of three distinct nucleated protoplasmic masses separated by cell plates formed in division *I* (nuclei of two larger protoplasmic masses not in focus). In other cases one or more small nuclei are not set off by cell plates from the major nuclei. It is conceivable that the condition depicted in figure 8, plate 6 resulted from a two-spindle sporocyte as in figure 5, plate 6, in which a minor spindle connects at right angles with the major spindle. In the other cases, however, the small nuclei may have

originated from univalents which lagged during anaphase *I*. Some sporocytes showed a great many nuclei grading in size from large to very minute. The very small nuclei probably represent reorganized chromatin fragments, since breaking up of the chromosomes during anaphase *I* is so obvious in some cells.

During interkinesis the dyad and monad chromosomes become invisible as such and the nucleus takes on a metabolic appearance. As the prophase *II* progresses the characteristic X-, H- or rod (monad)-shaped chromosomes become evident. Frequently, in those cells which possess small nuclei besides a large one, a similar prophase *II* transformation appears to be going on within these small nuclei. Such is the case shown in figure 7, plate 6. The small nucleus, about which a spindle is forming, contains a dyad chromosome. Consequently more than two metaphase *II* spindles may occur within a single sporocyte (figure 13, plate 6). In both acetocarmine and sectioned material sporocytes were seen with all the chromosomes in a single metaphase *II* spindle (figure 12, plate 6).

In general, the second meiotic mitosis appears much freer from irregularities than the first. There is very little fragmentation and comparatively little lagging of chromosomes. In many cases the wall laid down during *I* disappears soon after its formation. In consequence, the spindles of *II* lie in a common mass of cytoplasm. Rather infrequently tripolar spindles were observed which had been formed from a partial fusion of the two metaphase *II* spindles (figure 9, plate 6).

In consequence of the irregularities attending division *I* and *II* a single sporocyte can produce from two to many spores, the nuclei of which contain various amounts of chromatin. These spores, in turn, may be uninucleate or, as is frequently the case, multinucleate, the nuclei being variable in size and probably in chromosome content. The pollen grains exhibit such size relationships as would be expected from the above description.

PLASMODIAL SPOROGENOUS TISSUE

In the triploid plant and its F_1 descendants the sporocytes within some anther loculi, instead of existing as well defined individual cells, showed various degrees of cytoplasmic fusion. All conditions from a partial union of a few adjacent cells to a complete loss of identity of the sporocytes were observed, the result in the latter case being a plasmodium which filled the entire anther cavity. In some plasmodia two or more nuclei were so close together that only a very thin layer of cytoplasm appeared to exist between them. In several instances two adjacent nuclei appeared to be fusing.

The nuclei in the plasmodium continue their prophase meiotic development, forming well defined diakinesis and metaphase *I* figures (text figure 2). Probably as the result of the closeness of nuclei in these plasmodial masses, metaphase *I* spindles connect in various ways. It is conceivable that some of the metaphase *I* spindles exhibiting a double number of chromosomes have arisen in this manner. It is also conceivable that other metaphase *I* spindles possessing the double number of chromosomes, the homologous members of which, however, show a close synaptic attraction, have arisen by an earlier prophase fusion of nuclei, or possibly even by a pre-meiotic fusion.

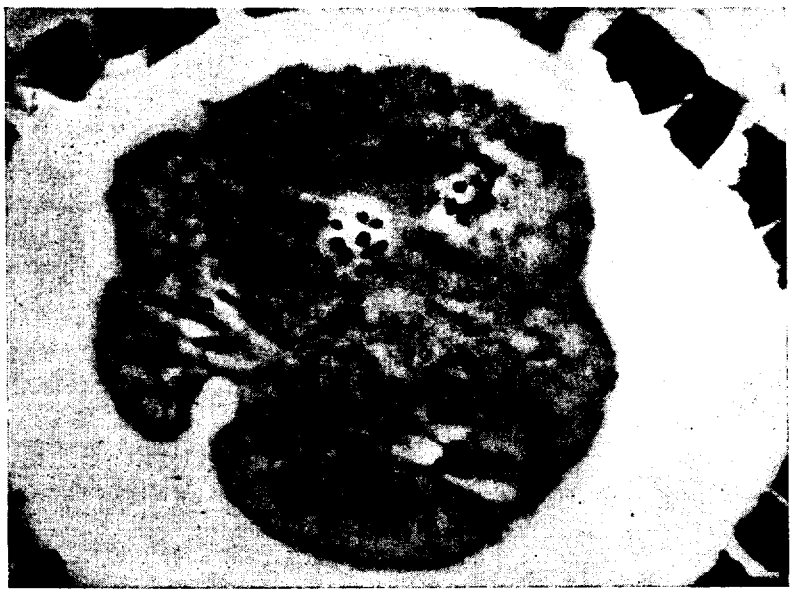

FIGURE 2.—Photomicrograph of plasmodium in anther showing 3 metaphase *I* spindles and one nucleus in late diakinesis.

As a result of the first meiotic division the plasmodium becomes divided into smaller masses separated by well defined cell plates.

CHROMATIN EXTRUSION IN SPOROGENOUS TISSUE

The breaking up of chromatin to form many small nuclei which become distributed in the cytoplasm was seen to occur in several stages of meiosis.

Sporocytes in prophase *I* exhibited numerous figures of "cytomixis" as described by many authors. Another striking prophase *I* phenomenon was the presence of small supernumerary nuclei distributed in the cytoplasm or closely associated with the main nucleus (figure 10, plate 6). It is pos-

sible, in some cases, that the small nuclei were formed from the main nucleus by budding (see SAKAMURA 1920). In other cases chromatin threads which have been seen extending through the nuclear membrane into the cytoplasm (figure 11, plate 6) may have given rise to some of these diminutive nuclei.

Extensive chromosome fragmentation occurring during anaphase *I* was observed in a number of sporocytes. Many small nuclei were observed in some sporocytes which obviously had been formed from reorganized chromosome fragments.

THE F_1 GENERATION

Because of the observed cytological behavior in the triploid individual, it was of great interest to follow the distribution of the chromosomes through future generations. Also, as little was known concerning the geneetic constitution of the three chromosomes of an homologous group, crosses were made to determine this to some extent. In almost every case where crosses were made the chromosome number and meiotic behavior of the plants used had been determined (see table 1). This was obviously necessary, as LONGLEY (1927) and RANDOLPH (1928) have shown that in many genetic cultures one or more extra chromosomes are present which are carried on to future generations.

Further indication that the extra chromosome in the F_1 individuals originated from the gametes in the triploid was seen in the contrast between the appearance and behavior of these F_1 individuals with extra chromosomes and in those extra chromosome individuals within genetic strains of maize. The extra chromosomes (when more than one extra chromosome is present it seems to be due to a reduplication of the same chromosome) running through some genetic strains of maize and found principally in Black Mexican sweet corn do not affect size, vigor or fertility to any noticeable degree. They are carried through in the eggs or the pollen. The extra chromosomes in the F_1 plants of the cross triploid $\times$ diploid, on the other hand, affect size, vigor and fertility and are carried only to a small extent through the pollen. In a $2n+1$ plant of Black Mexican the chromosomes do not, so far as I am aware, form $9^{II}+1^{III}$, but always $10^{II}+1^{I}$. This is quite in contrast with the $2n+1$ F_1 plants from the cross diploid $\times$ triploid, which form most frequently $9^{II}+1^{III}$. On the basis of studies of chromosome morphology made by Doctor RANDOLPH in extra chromosome plants of Black Mexican sweet corn and in some genetic strains of maize, it is believed that this extra chromosome is not a whole duplicate of any one member of the haploid set of ten chromosomes. On the other hand, the

extra chromosome in the 2n+1 F_1 individuals of the cross diploid × triploid is a true duplicate of one member of the haploid set. The same chromosome is very likely involved in all the usual 2n+1 plants of Black Mexican sweet corn and genetic strains of maize. The extra chromosome in the several 2n+1 F_1 individuals of the cross diploid × triploid is not always the same, but represents different members of the haploid set.

Table 1 was constructed to show what crosses were made and the general results obtained. All the available material resulting from these crosses has not yet been investigated, but a sufficient amount has been examined to give an indication of what, in general, has taken place.

As it was desired to obtain the best results with the least amount of pollen, care was taken to collect the pollen soon after shedding. In every cross sufficient pollen was used to pollinate a whole ear in an ordinary maize plant. As the triploid plant had several good tillers, much pollen was available even though many anthers never opened. The fact that only a few kernels developed on an ear as a result of these crosses could not, then, be attributed to a lack of sufficient pollen.

The occurrence of a selection of gametes containing certain chromosome complements (in the cases where triploid pollen was used in crossing on to diploid plants) was markedly indicated by the few kernels on an ear and the chromosome number shown by the individuals coming from these kernels (table 5). Where there are few kernels on an ear the 10-chromosome carrying gametes apparently have been successful, whereas the extra-chromosome carrying gametes probably have not functioned in fertilization. In other crosses where many kernels were found on an ear ($36_2 \times 56_2$, table 5) not only the 10-chromosome carrying gametes functioned but also many of the 10+1 and 10+2-chromosome gametes. Why it is that in all cases where a sufficient amount of pollen was used, there appeared such a dissimilar selectivity toward certain chromosome-carrying gametes among the different plants, is not known.

When the cross triploid ♀ × diploid ♂ is made, the results are strikingly different (table 5). Here, apparently, the eggs containing various chromosome numbers function. However, they do not function perfectly, as relatively few kernels developed on an ear. Since microsporogenesis is known to produce such varied types of cells with regard to chromosome complement, it is conceivable that megaspores in many ovules are incapable of developing a functioning gametophyte. The plants which were least vigorous contained the highest number of extra chromosomes. These grew from small underdeveloped kernels which had been carefully treated to induce germination. As there were many of them on the ear, it is probable

TABLE 1

CROSS, 1925	CHROMOSOME NUMBER OF ♀ PARENT	CHROMOSOME NUMBER OF ♂ PARENT	NUMBER OF KERNELS ON EAR	CHARACTER OF F1 KERNELS	F1 CULTURE NUMBER: GREENHOUSE	F1 CULTURE NUMBER: FIELD	NUMBER OF KERNELS PLANTED	NUMBER OF PLANTS DEVELOPED	CHROMOSOME NUMBER OF F1 PLANTS: 2n	2n+1	2n+2	2n+3	2n+4	2n+5	2n+6	2n+7	2n+8	2n+9	3n	11II + 2n+2
56_3+	10^{III}	10^{III}	6	1 purple sugary 3 colorless sugary 2 underdeveloped		96 97	6	0	..	..	..	..	..	..	..	..	..	..	..	..
$56_2 \times 33_6$ *ABp₁ l₉ jY*	10^{III}	10^{II}	34	8 purple starchy 26 colorless starchy	68 69	94 95	31	11	..	1	3	1	3	1	..	1	..	..	..	..
$56_2 \times$ E14–871$_3$	10^{III}		10	4 colorless starchy 6 poorly developed	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
56_2 kernels formed in main and tiller tassels.	10^{III}	?	22	9 purple starchy 4 colorless starchy 2 colorless sugary 7 underdeveloped	64 65 66 67	..	7	3	..	1	1	1	..	..	..	..	..	..	..	..
$2_7 \times 56_2$ *A b p₁*	?	10^{III}	0		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$16_9 \times 56_2$ *a C R $S_u W_a$ $l_9 y$ b p_1*	12^{II}	10^{III}	0		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$17_2 \times 56_2$ *ACr S_u b p_1*	10^{II}	10^{III}	17	9 purple starchy Y 8 colorless starchy Y	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$20_{12} \times 56_2$ *A P l_9*	?	10^{III}	0		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$21_{14} \times 56_2$ *ACR p_r b p_1*	10^{II}	10^{III}	1	1 purple starchy	..	81	1	1	1	..	..	..	..	..	..	..	..	..	..	..
$23_8 \times 56_2$ *a b p_1 C R*	10^{II}	10^{III}	9	4 purple starchy Y 5 colorless starchy Y	77	82 83	8	6	6	..	..	..	..	..	..	..	..	..	..	..
$24_{18} \times 56_2$ *Ac R b p_1*	10^{II}	10^{III}	6	4 purple starchy 1 colorless starchy 1 outside pollination	78	84	4	4	3	..	..	..	..	..	..	..	..	..	..	1
$25_1 \times 56_2$ *ACr s_u*	13^{II}	10^{III}	2	2 colorless, underdeveloped	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$26_1 \times 56_2$ *ACr r_a y*	10^{II}	10^{III}	22	9 purple starchy 13 colorless starchy	73 74	85 86	13	8	6	1	..	..	..	..	..	..	..	..	1	..
$27_{13} \times 56_2$ *Abp₁ l_ay*	10^{II}	10^{III}	0		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$28_4 \times 56_2$ *Abp₁ l_a*	10^{II}	10^{III}	0		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$30_{14} \times 56_2$ *Abp₁ z_a j*	?	10^{III}	1	1 purple underdeveloped	..	87	1	0	..	..	..	..	..	..	..	..	..	..	..	..
$31_1 \times 56_2$ *j l_9*	?	10^{III}	0		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$33_6 \times 56_2$ *ABp₁ l_aj S_u Y*	10^{II}	10^{III}	7	3 yellow starchy 4 badly infected, broken kernels	70	93	3	2	2	..	..	..	..	..	..	..	..	..	..	..
$34_{77} \times 56_2$ Anther ear	?	10^{III}	3	3 yellow starchy	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$36_2 \times 56_2$ *AcR s_u b p_1 y*	10^{II}	10^{III}	49	19 purple sugary 30 colorless sugary	71 72	88 89	20	10	3	5	2	..	..	..	..	..	..	..	..	..
$38_2 \times 56_2$ *ACr g b p_1*	10^{II}	10^{III}	18	4 purple starchy 14 colorless starchy	75 76	90 91	8	6	6	..	..	..	..	..	..	..	..	..	..	..
$44_{12} \times 56_2$ *g_1*	?	10^{III}	0		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$45_9 \times 56_2$ *g_1*	10^{II}	10^{III}	10	4 purple starchy Y 6 colorless starchy Y	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
$51_5 \times 56_2$ *b, P^{rr}*	?	10^{III}	15	Red pericarp, starchy 5 purple, 10 colorless	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
E13–533 $\times 56_2$		10^{III}	6	6 teosinte-like	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
E14–871$_3 \times 56_2$		10^{III}	1	1 teosinte-like	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
R191$_1 \times 56_2$		10^{III}	13	13 purple starchy Y	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
R251$_2 \times 56_2$		10^{III}	3	3 yellow sugary	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
R250$_6 \times 56_2$		10^{III}	2	2 purple sugary	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
R251$_2 \times 56_2$ tiller		10^{III}	1	1 colorless sugary Y	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

* See note in table 2

TABLE 2

Culture numbers of F_1 individuals with their respective chromosome number.

10^{II}	$9^{II}+1^{II}$	$8^{II}+2^{III}$	$7^{II}+3^{III}$	$6^{II}+4^{III}$	$5^{II}+5^{III}$	$4^{II}+6^{III}$	$3^{II}+7^{III}$	$2^{II}+8^{III}$	$1^{II}+9^{III}$	10^{III}	11^{II*}
73_1	67_1	67_2	65_1	94_4	94_2		94_3			73_2	84_2
74_1	68_2	$68_{3,4}$	95_1	$95_{2,3}$							
75_1	$72_{2,3}$	72_1									
$76_{1,2}$	86_2	88_4									
$77_{1,2}$	$88_{1,3}$	94_1									
$78_{1,2}$	89_1										
81_1											
$82_{1,2,3}$											
83_1											
84_1											
$85_{1,2,3}$											
86_1											
$88_{2,5}$											
89_2											
90_1											
$91_{1,2}$											
$93_{1,2}$											

* This individual probably came from an outside pollination. The two extra chromosomes are similar to those found in extra chromosome plants of Black Mexican sweet corn.

FIGURE 3.—Photograph of F_1 plants grown in the field resulting from the cross triploid ♀ × diploid ♂ arranged according to chromosome complement. Plant no. 1, 94_1; no. 2, 95_1; no. 3 95_2; no. 4, 95_3; no. 5, 94_4; no. 6, 94_2; no. 7, 94_3.

that if all could have been induced to germinate a wider range of chromosome number in the F_1 would have been found. Thus the limiting factor in

FIGURE 4.—Photograph of F_1 plants from reciprocal cross (diploid ♀ × triploid ♂) to that shown in text figure 3. Both individuals were diploid. Plant no. 8, 93_2; no. 9, 93_1.

some cases is probably not the inability of the female gametophyte to function, but rather the capacity of the chromosome complement within the embryo to participate in growth and development.

The marked effect of the presence of extra chromosome on the appearance of the plant is graphically represented by text figures 3, 4, 5 and 6. These photographs were made after the plants had matured ears. In consequence the leaves are dried and curled. However, the relative sizes of the plants containing varying chromosome numbers are preserved.

Two plantings of F_1 kernels were made, one in the spring of 1926 in the greenhouse and one in the summer of 1926 in the field. For a summary of germination results see table 3.

TABLE 3

Results of germination.

Origin of F_1 kernels	GREENHOUSE		FIELD	
	Kernels planted	Mature plants	Kernels planted	Mature plants
56_2 tassel	7	3		
$56_2 \times 33_5$	10(3 died)†	4	21*	7
56_2 selfed			6	0
$21_{14} \times 56_2$			1	1
$23_8 \times 56_2$	2	2	6	4
$24_{18} \times 56_2$	2	2	2	2
$26_1 \times 56_2$	5(2 died)†	3	8	5
$30_{14} \times 56_2$			1	0
$33_5 \times 56_2$	1(died)†	0	2	2
$36_2 \times 56_2$	10(5 died)†	3	10	7
$38_8 \times 56_2$	5(1 died)†	4	3	2

* 9 well developed kernels gave rise to 4 mature individuals, one with $8^{II}+2^{III}$, one with $7^{II}+3^{III}$ and two with $6^{II}+4^{III}$.

12 underdeveloped kernels gave rise to 3 mature individuals with chromosome numbers $6^{II}+4^{III}$, $5^{II}+5^{III}$ and $3^{II}+7^{III}$ respectively.

† Plants began development but died from "damping off" in seedling stage.

MEIOSIS IN F_1 INDIVIDUALS

The behavior of the chromosomes during meiosis was studied in fifty F_1 individuals. When diploid individuals were pollinated with pollen from the triploid, twenty of the thirty-seven plants examined showed ten pairs of

chromosomes at diakinesis and metaphase *I*. The meiotic behavior in these plants was similar in all observed details to that in ordinary diploid individuals. In size and vigor they surpassed those F_1 individuals which possessed one or more extra chromosomes (compare plant No. 14, text figure 6 with its sib, plant No. 10, text figure 5; plants 15, 16 and 18, text figure 6 with their sibs, plants 11, 12 and 13, text figure 5).

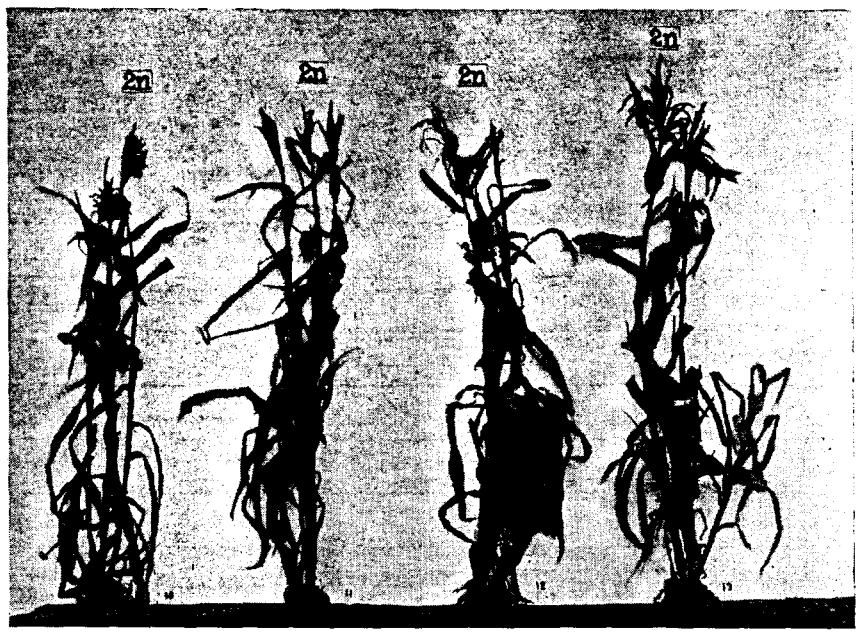

FIGURE 5.—Diploid individuals resulting from cross diploid ♀ × triploid ♂. Plant no. 10, 86_1; no. 11, 88_2; no. 12, 88_5; no. 13, 89_2.

Meiosis in 2n+1 individuals

Out of fifty F_1 individuals examined, eight showed the presence of one extra chromosome: two out of thirteen in the cross triploid ♀ × diploid ♂ and six out of thirty-seven in the reciprocal cross, diploid ♀ × triploid ♂. Cytological examination indicated that different chromosomes of the haploid set we involved in the several 2n+1 plants. However, the 2n+1 plants did not show characteristic differences that could be ascribed to certain chromosomes of the set.

In describing meiosis in these plants reference will be made, at times, to figures from plants which contained more than one extra chromosome. Since similar conditions existed in all the extra chromosome plants, one

figure will suffice for illustration. This has been done to avoid repetition of figures illustrating similar phenomena.

There were fewer meiotic irregularities in these individuals than in those containing more than one extra chromosome. As in all F_1 extra chromosome plants, a variation in synaptic expression of the extra chromosome was noticed. In the 2n+1 plants $9^{II}+1^{III}$ (figure 11, plate 2) was found about twice as frequently as $10^{II}+1^{I}$ (figures 12 and 13) in both diakinesis and metaphase *I* (table 4). The appearance and position of the univalent during metaphase *I* are rather varied. The univalent may be found in any region of the spindle. It occasionally is not included in the spindle but

FIGURE 6.—Extra chromosome individuals resulting from cross diploid ♀ × triploid ♂. These are sibs of those plants shown in text figure 5. Plant no. 14, 86_2; no. 15, 88_1; no. 16, 88_3; no. 17, 88_4; no. 18, 89_1.

lies in the cytoplasm. When a univalent lies in or near the plate it may split simultaneously with the disjunction of the bivalents, or it may lag until the bivalents have completely disjoined and have passed toward either pole, when, in turn, it may split, the halves separating and advancing toward opposite poles. These may or may not be included in the reorganizing nuclei (figures 9, 10, 24, 28 and 34). The univalent may remain unsplit at the equator and subsequently be left in the cytoplasm as a chromatic mass. When a trivalent is present, on the other hand, disjunction of the three homologues and the passage of two toward one pole and one toward the other pole seem to be quite regular.

Interkinesis most frequently shows two well organized nuclei lying in cytoplasmic masses separated by a cell plate. Occasionally, in the cyto-

plasm of one or both cells, there lie one or more chromatic bodies distinguishable as dyad or monad. Besides the two major nuclei one or more very small nuclei may be found in the cytoplasm of one or both cells.

TABLE 4

Frequency of appearance of different synaptic combinations in F_1 extra chromosomes individuals.

PLANT	SYNAPSIS	DK.	M_I	PLANT	SYNAPSIS	DK.	M_I
86_2	$9^{II}+1^{III}$	8	28	94_3	$3^{II}+7^{III}$	5	8
	$10^{II}+1^{I}$	4	10		$4^{II}+6^{III}+1^{I}$	4	8
					$5^{II}+5^{III}+2^{I}$	2	5
88_1	$9^{II}+1^{III}$		5		$6^{II}+4^{III}+3^{I}$	2	2
	$10^{II}+1^{I}$	1	7		$7^{II}+3^{III}+4^{I}$		
					$8^{II}+2^{III}+5^{I}$		
88_3	$9^{II}+1^{III}$	9	40		$9^{II}+1^{III}+6^{I}$		2
	$10^{II}+1^{I}$	6	12		$10^{II}+7^{I}$		
89_1	$9^{II}+1^{III}$	1	7	95_1	$7^{II}+3^{III}$	1	33
	$10^{II}+1^{I}$		4		$8^{II}+2^{III}+1^{I}$	1	41
					$9^{II}+1^{III}+2^{I}$		27
	$8^{II}+2^{III}$	6	8		$10^{II}+3^{I}$		6
88_4	$9^{II}+1^{III}+1^{I}$	4	7				
	$10^{II}+2^{I}$	1	2	95_2	not recorded		
	$8^{II}+2^{III}$		20				
94_1	$9^{II}+1^{III}+1^{I}$	1	8				
	$10^{II}+2^{I}$		2				
					$6^{II}+4^{III}$		6
	$5^{II}+5^{III}$		7		$7^{II}+3^{III}+1^{I}$		11
	$6^{II}+4^{III}+1^{I}$		6		$8^{II}+2^{III}+2^{I}$		10
	$7^{II}+3^{III}+2^{I}$		3	95_3	$9^{II}+1^{III}+3^{I}$		3
	$8^{II}+2^{III}+3^{I}$	1	1		$10^{II}+4^{I}$		1
	$9^{II}+1^{III}+4^{I}$		2				
94_2	$10^{II}+5^{I}$		0		$6^{II}+4^{III}$		18
	$9^{II}+7^{I}$		1		$7^{II}+3^{III}+1^{I}$		12
	$4^{II}+3^{III}+8^{I}$	1	1	94_4	$8^{II}+2^{III}+2^{I}$		4
	$3^{II}+2^{III}+13^{I}$	1			$9^{II}+1^{III}+3^{I}$		
	$2^{II}+1^{III}+18^{I}$		1		$10^{II}+4^{I}$		
	$1^{II}+1^{III}+20^{I}$		1				
	25^{I}		3				

Dk. = diakinesis; M*I* = metaphase *I*.

Since there were many 10–11 anaphase *I* chromosome distributions, this same relation appeared in pairs of prophase *II* nuclei. The second meiotic mitosis proceeded with little irregularity. Occasionally a dyad chromosome lagged in anaphase *II* with or without subsequent separation of its members; or, as the anaphase advanced, a monad ceased to keep pace and was

left out of the telophase nucleus. Sometimes such a lagging chromosome, whether a dyad or a monad, became included in the forming wall (figure 30). Some cells possessed a second small spindle, oriented at various angles or connected with the major spindle.

In consequence of such meiotic behavior we most frequently encountered complete quartets of spores, each spore containing one well formed nucleus. Occasionally other small nuclei or chromatic bodies were observed in the cytoplasm. Only seldom did a sporocyte give rise to more than four spores.

Unusual meiotic phenomena in 2n+1 individuals

Some anther loculi in both greenhouse and field plants were filled with a plasmodial mass including either prophase *I* nuclei, like or unlike in size, or metaphase *I* figures, free or connecting with each other at various angles (figure 19). The chromosome number in the various figures was not always the same. Some had more than the normal number for the plant in question and some less (upper spindle, figure 19). In one case the number amounted to four times that expected, the spindle being perfectly formed and the chromosomes regularly arranged. There appeared, in a few of these plasmodial sporogenous masses, nuclei containing amounts of chromatin not in accordance with their various sizes. A large nucleus might contain but a single chromatic thread lying against the nuclear membrane, nearly the whole volume, of the nucleus being karyolymph. An adjacent nucleus, small in volume might be densely packed with a chromatin spireme. In the same plasmodium all states between these two existed.

In figure 17 is shown a metaphase *I* spindle containing $20^{II}+2^{I}$, double the expected number; this was seen in a well rounded sporocyte. Figure 18 shows a well formed spindle containing $40^{II}+4^{I}$, or four times the expected number.

Fragmentation appeared in these and other F_1 plants. It was most evident during anaphase *I* (figure 20). The fragments vary in size from a mere speck of chromatin to a large portion of a dyad. Appearances indicate that some of these fragments have the ability to divide. This is observable in the chromosome fragments at the center of the spindle (figure 20).

Meiosis in 2n+2 individuals

Out of fifty F_1 individuals examined, six possessed two extra chromosomes belonging to two different homologous groups. In the direct cross triploid ♀ ×diploid ♂ four out of thirteen showed two extra chromosomes; in the reciprocal cross, two out of thirty-seven. These plants were smaller and less vigorous than their sibs with one extra chromosome.

TABLE 5 (Abridgment of Table 1)

CROSS	NUMBER OF KERNELS ON EAR	NUMBER OF KERNELS PLANTED	NUMBER OF PLANTS DEVELOPED	2n 10^{II}	2n+1 $9^{II}+1^{III}$	2n+2 $8^{I}+2^{III}$	2n+3 $7^{II}+3^{III}$	2n+4 $6^{I}+4^{III}$	2n+5 $5^{II}+5^{III}$	2n+6	2n+7 $3^{II}+7^{III}$	2n+8	2n+9	3n 10^{III}	2n+2† 11^{II}
56_2 tassel	22	7	3		1	1	1								
$56_2 \times 33_5$	34	31	11*		1	3	1	3	1		1				
56_2 selfed	6	6	0												
Total		44	14		2	4	2	3	1		1				
$21_{14} \times 56_2$	1	1	1	1											
$23_8 \times 56_2$	9	8	6	6											
$26_1 \times 56_2$	22	13	8	6	1									1	
$24_{18} \times 56_2$	6	4	4	3											1
$30_{14} \times 56_2$	1	1	0												
$33_5 \times 56_2$	3	3	2	2											
$36_2 \times 56_2$	49	20	10	3	5	2									
$38_8 \times 56_2$	18	8	6	6											
Total		58	37	27	6	2								1	1
Grand Total		102	51	27	8	6	2	3	1		1			1	1

* Chromosome number of one plant not obtained.
† See note in table 2.

Meiosis in these plants was similar in most details to that of the 2n+1 individuals with the added complication of the one extra chromosome; thus making the observed irregularities more numerous than in the 2n+1 plants. The univalents acted similarly but independently of one another. During diakinesis and metaphase *I* (figure 22, plate 3) were seen most frequently $8^{II}+2^{III}$, less frequently $9^{II}+1^{III}+1^{I}$ (figure 21) and least frequently $10^{II}+2^{I}$ (see table 4).

Because of the extra chromosome, anaphases were markedly more irregular than in the 2n+1 plants. Here we frequently found 11 chromosomes passing to each pole, although 10–12 distributions were numerous. The lagging of one or two chromosomes, the lagging and splitting of one or two, or combinations of these two types were rather numerous. Figure 24 illustrates the lagging and splitting of one dyad in a spindle where ten chromosomes have gone to one pole and eleven to the opposite pole. Appearances in telophase *I* and prophase *II* were similar to those in the 2n +1 plants. Figure 31, a prophase *II*, in which the chromosomes in the left cell are farther advanced than those in the right, indicates that a 10–12 distribution in anaphase *I* must have taken place. Such a prophase as that in the right half of figure 31 might be followed by an anaphase *II* distribution like that illustrated in figure 29. More frequently, however, the anaphases of *II* were less regular, being marked by the lagging of one or two chromosomes which eventually become excluded from the reorganizing nuclei. In consequence, the spores frequently appeared much as in figure 30. Sometimes an irregular spore quartet, as illustrated in figure 25, was formed.

One greenhouse plant (68_3) exhibited more striking irregularities in meiotic phenomena than any other individual examined. Many anthers possessed one continuous plasmodium in which lay nuclei ranging in size from very minute to those two and three times the volume of the normal nucleus. These, in turn, probably gave rise to plasmodial sporogenous masses in which lay spindles of all sizes containing from very few chromosomes to more than four times the normal number for the plant. In one huge sporocyte there were two parallel metaphase *I* spindles, in each of which lay four times the normal number of chromosomes. The chromosomes were associated as bivalents, trivalents, quadrivalents, quintivalents and sexivalents. Unfortunately, the slide was damaged before a drawing was made.

In this plant some sporocytes exhibited metaphase *I* figures with twice the normal number of chromosomes. In all previous cases in other plants where tetraploid metaphase *I* spindles were observed, the chromosomes

of the four sets gave no synaptic evidence of homology (see figures 17 and 18). Here, however, the homologies were frequently expressed by the synaptic union of four chromosomes to form a quadrivalent or of six to form a sexivalent (it is to be remembered that this plant showed, normally, $8^{II}+2^{III}$). Not all the chromosomes of the four sets necessarily formed such synaptic combinations, for two homologous bivalents sometimes appeared distinctly separated. Such a case is illustrated in figure 27, which was drawn from a remarkably clear figure with $2^{VI}+6^{IV}+4^{II}$. Figure 28 represents an anaphase *I* distribution of chromosomes in a tetraploid sporocyte including a lagging bivalent, a lagging and splitting dyad and two lagging but separating monads.

Figure 26 shows a metaphase *I* spindle from this same plant which contains 1 bivalent less than normal, that is, $7^{II}+2^{III}$.

Meiosis in plants with 2n+3 to 2n+7 chromosomes

A reference to table 5 will show that individuals with more than two extra chromosomes appeared only in the cross triploid ♀ × diploid ♂ (with the exception of a new triploid). There were two plants with $7^{II}+3^{III}$, three with $6^{II}+4^{III}$, one with $5^{II}+5^{III}$, and one with $3^{II}+7^{III}$. The presence of extra chromosomes was suggested in the small size and decreased vigor of these F_1 individuals before meiosis was observed (see text figure 3).

Since synapsis was so varied, it was of interest to determine the percentage of bivalents, trivalents and univalents in the various diakinesis and metaphase *I* figures of each plant. Reference to table 4 will show that there was a general tendency on the part of the univalents to be associated with the bivalents to form trivalents at diakinesis and metaphase *I* in a good percentage of the cases.

Figure 32, plate 4, shows $7^{II}+3^{III}$, while figure 33 represents a metaphase *I* with $8^{II}+2^{III}+1^{I}$. In figure 36 we observe $8^{II}+1^{III}+4^{I}$, indicating that there has been non-synapsis or early disjunction of one of the bivalents ordinarily present as such. A metaphase *I* figure in plant 95_2 with four extra chromosomes is shown in figure 39; here there are clearly $6^{II}+4^{III}$.

Plant 95_3 with four extra chromosomes is represented by figure 37, in which we find $6^{II}+4^{III}$. When it was determined that photography could be of service in describing the results, this same figure was photographed (figure 14, plate 6). In an adjacent sporocyte (text figure 7) we find $7^{II}+3^{III}+1^{I}$, while in still another sporocyte we see $10^{II}+4^{I}$ (figure 15, plate 6).

A metaphase *I* with $3^{II}+7^{III}$ is shown in figure 38, which was drawn from a sporocyte of a 2n+7 individual.

Anaphases in these plants were very similar to those already described

for other F_1 extra-chromosome individuals, with the added complication of more univalents and consequently more irregular behavior. In an anaphase *I* (figure 34) of plant 95_1 (2n+3) two lagging dyads show clearly the split in preparation for *II*, while the components of two other dyads have already commenced to separate.

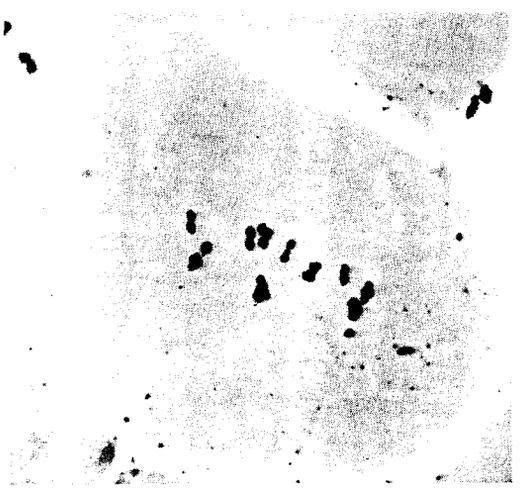

FIGURE 7.—Photomicrograph of microsporocyte of 2n+4 individual showing 7 bivalents, 3 trivalents and 1 univalent. See photographs of adjacent sporocytes, figures 14 and 15, plate 6. From an aceto-carmine smear preparation.

Since irregularity increases in proportion to the number of extra chromosomes present, the variation in spore formation increases accordingly. Giant spores, dyads, quartets and polyspory with and without extra, small nuclei or chromatin masses were repeatedly observed.

F_1 triploid plant

In the greenhouse plants there appeared a new triploid from the cross diploid ♀ × triploid ♂. Since meiosis in the new triploid was essentially similar to that of the triploid already described, no further discussion will be given. Figure 40 represents a metaphase *I* in which there are 10^{III}.

Irregular synapsis in a 2n+5 individual

Since plant 94_2 (2n+5) showed an almost complete series of non-synapses of homologous chromosomes during diakinesis and metaphase *I*, ranging from $5^{II}+5^{III}$ to 25^{I}, it has been considered separately. In many of the sporocytes of an anther we found the synaptic condition to be very similar to that already described for other extra-chromosome F_1 indivi-

duals, that is, $5^{II}+5^{III}$, $6^{II}+4^{III}+1^{I}$ to $10^{II}+5^{I}$ (figure 41). Besides this, non-synapsis extended to the bivalents themselves, forming, for instance, $9^{II}+7^{I}$ (figure 42) or $4^{II}+3^{III}+8^{I}$ (figure 43).

The appearance of the diakinesis figures (figure 43) points toward a possible early disjunction as an explanation, since the members of many bivalents and trivalents were specially far apart, remaining connected only by long, fine threads.

Anaphases vary in appearance according to the number of univalents present. When there are few univalents the figures are quite normal. When there are many univalents there is no well organized equatorial plate (figure 45, $1^{II}+23^{I}$; figure 46, $1^{II}+1^{III}+20^{I}$; figure 44, 25^{I}) the chromosomes being distributed throughout a greater part of the spindle.

We have, at present, no satisfactory explanation of this appearance. It is difficult to explain why such wide variations in synaptic expression occur in sporocytes of the same anther or of other anthers at the same stage of development. In the summer of 1926, under field conditions, RANDOLPH (1928) examined a number of inbred strains which were showing this non-synaptic phenomenon in many sporocytes. Normally in these individuals there are 10^{II} at metaphase *I* and meiosis is regular. However, in those diploid plants which showed some sporocytes with varying degrees of non-synapsis the univalents thus formed behaved much as they did in the extra-chromosome F_1 individuals and in hybrids in general. They lagged, or lagged and split, giving appearances of irregularity in a number of sporocytes. Other sporocytes in the same anther were perfectly normal in appearance and behavior.

Non-synapsis at diakinesis, whether it represents a true non-synapsis or merely an early disjunction, is caused in some cases by conditions other than lack of homology of the chromosomes present.

The F_1 extra-chromosome individuals described in this paper have been selfed and crossed for further cytological investigations to be reported later.

GENETIC INVESTIGATIONS

The kernels of culture 56 in which the triploid plant arose were planted for use as a sugary tunicate stock. In consequence, no particular attention was paid to the color of the kernels other than to note that a segregation for purple and white aleurone had occurred on the ear from which they had come. Since the culture was also segregating for the plant color factor *A*, little could be concluded directly about the constitution of the triploid itself. It was known to be phenotypically dilute sun red, tunicate and sugary.

Since three sets of chromosomes were present, it was desired to know what the genetic constitution of the triploid might be with respect to certain genetic factors, and how these might be carried to future generations. For this reason pollen of the triploid was placed upon silks of several genetic "testers" (see table 1) whose mirosporocytes had been examined to detect the possible presence of extra chromosomes or irregular behavior.

One ear of the triploid plant was used for the cross $56_2 \times 33_5$, the reciprocal cross ($33_5 \times 56_2$) being made also. A second ear was selfed and a third ear on a tiller was used in the cross triploid × tetraploid (perennial teosinte).

It will be seen by an examination of table 1 that very few kernels developed as a result of most of the crosses. If we disregard the possible selective germination of the F_1 kernels carrying extra chromosomes, it will appear on examination of table 5 that in most crosses the male gametes from the triploid which functioned possessed ten chromosomes.

In the crosses $21_{14} \times 56_2$, $23_8 \times 56_2$ and $33_5 \times 56_2$ (table 5) very few kernels developed on the ears. All the plants that grew to maturity from these crosses possessed but ten pairs of chromosomes. In certain crosses, namely, $26_1 \times 56_2$ and $36_2 \times 56_2$ (table 5) where relatively more kernels developed on an ear, the F_1 plants coming from these kernels showed not only diploids but some 2n+1 and 2n+2 individuals. This suggests that in the former case only the pollen grains carrying the haploid set of chromosomes functioned, while in the latter case not only the haploid pollen functioned but also the haploid+1 and some of the haploid+2 pollen, therefore producing more kernels on the ears.

Before beginning a discussion of the results obtained it would be well to outline briefly the expected diploid × triploid ratios, assuming random assortment of the extra chromosomes in the triploid with no selection of pollen or of F_1 chromosome combination. It is known from the observations of meiosis in the triploid that pollen carrying various chromosome numbers was formed. Assuming, for descriptive purposes, a factor *A* and its allelomorph *a*, we can say that if the triploid were homozygous for *A* (*AAA*), that is, triplex (BLAKESLEE, BELLING and FARNHAM 1920), the F_1 would be, phenotypically, *A*. If the triploid had the constitution *AAa* (duplex) the expected gametic ratio would be 2*A*: 1*AA*: 2*Aa*: 1*a*, and when crossed to *a* it would give, phenotypically, 5*A*: 1*a*. However, if the triploid were *Aaa* (simplex) the gametic ratio would be 1*A*: 2*Aa*: 2*a*: 1*aa*, and the backcross phenotype ratio 1*A*: 1*a*. If the triploid were homozygous recessive (nulliplex) the backcross would be totally recessive, phenotypically.

If, now, there is a decided selectior against the gametes carrying extra chromosomes, the functional gametic ratio becomes modified accordingly. In the case of *AAa* (duplex) eliminat:on of the extra chromosome carrying gametes would bring the functioning gametic ratio to $2A:1a$. In the case of *Aaa* (simplex) such a selection would give a functioning gametic ratio of $1A:2a$. Gametic selection in the reciprocal crosses of the diploid × triploid has been discussed in connection with the cytology of the F_1 individuals. We have seen that meiosis in diploid individuals usually results in the production of haploid spores and in consequence haploid gametes containing ten chromosomes. Meiosis in the triploid, however, results in the production of microspores containing various chromosome numbers. When pollen from the triploid is used in crossing on to silks of a diploid individual the pollen grains that seem to be functionally successful contain for the most part 10 chromosomes, or occasionally 10+1 or 10+2. Hence, from such a cross we should expect a duplex or simplex factorial condition in the triploid to appear in the backcross in the phenotypic ratios of $2A:1a$ or $1A:2a$ respectively. In the cross triploid ♀ × diploid ♂, on the other hand, we have seen that there has been no such marked elimination of the extra chromosome carrying gametes of the triploid. In consequence the ratios should be expected to show some approach to those indicated in the preceding paragraph.

Although not all the F_1 kernels have been grown and the genetic data are few, the results so far obtained and outlined below tend to confirm this expectation.

The triploid was triple recessive or nulliplex for the plant color factors *b* and p_l (Emerson 1921); since it was dilute sun red and gave only dilute sun red individuals when crossed to plants which were homozygous Abp_l. Likewise it was nulliplex for the factor s_u responsible for sugary endosperm (see table 1, $36_2 \times 56_2$ and 56_2 selfed) and the endosperm factor *y* which is the allelomorph of *Y* responsible for yellow endosperm (see table1, $36_2 \times 56_2$) (Correns 1901, East and Hayes 1911).

The evidence points toward the fact that the triploid was simplex for the factors *C* and *R*, two complementary aleurone color factors (Emerson 1918). Considering the factor *C*, which with *A* and *R* seems to be responsible for the presence of colored aleurone, the following ratio of F_1 kernel color was noted when the triploid was crossed to an *AAccRR* or so-called *C*-tester (table 6).

Since in these crosses there was a selection against pollen carrying the higher numbers of chromosomes expected on the assumption of random assortment, the F_1 ratio, according to our interpretation, should approach

TABLE 6

CROSS *AAccRR*×triploid	F1 ALEURONE COLOR	
	Colored	Colorless
$24_{18}\times56_2$	4	1
$36_2\times56_8$	19	30
Total	23	31

a 1:2 if the triploid was simplex for the factor *C*. Although the data are few, this ratio is approximated. Certainly it does not approach the duplex 2:1 ratio.

With reference to the factor *R*, the simplex condition in the triploid was suggested by the results of the following crosses which were made to *R* testers (*AACCrr*) (table 7).

TABLE 7

CROSS *AACCrr*×triploid	F1 ALEURONE COLOR	
	Colored	Colorless
$17_4\times56_2$	9	8
$25_1\times56_2$		2
$26_1\times56_2$	9	13
$38_8\times56_2$	4	14
Total	22	37

Since the functioning male gametes are predominantly carrying only ten chromosomes (table 5), the results recorded in table 7 can best be interpreted as a 1:2 modified simplex ratio.

Fortunately, the triploid possessed the dominant plant factor tunicate (T_u) COLLINS 1917). Direct and reciprocal crosses were made to the double recessive (t_ut_u). Since there was no obvious selection against gametes carrying higher chromosome numbers in the cross triploid ♀ × diploid ♂, the unmodified triploid ratios would be expected to appear in the F_1 of this cross, that is, if the triploid were simplex for T_u, the ratio would be a 1:1, if duplex, 5:1. In the reciprocal cross, since selection against the higher chromosome gametes occurs, the modified ratio should appear, that is, if simplex a 1:2, if duplex, a 2:1 ratio. The following are the results obtained in the direct and reciprocal crosses (tables 8 and 9).

TABLE 8

F_1 triploid ♀ × diploid ($t_u t_u$) ♂.

CROSS	TUNICATE	NON-TUNICATE
$56_2 \times 33_5$	8	2

TABLE 9

F_1 diploid ($t_u t_u$) ♀ × triploid ♂.

CROSS	TUNICATE	NON-TUNICATE
$21_{14} \times 56_2$	0	1
$23_8 \times 56_2$	2	3
$24_{18} \times 56_2$	2	2
$26_1 \times 56_2$	7	1
$33_5 \times 56_2$	1	1
$36_2 \times 56_2$	7	3
$38_8 \times 56_2$	4	2
Totals	23	13

The results tabulated above afford evidence for a duplex condition of T_u ($T_u T_u t_u$) in the triploid. Although the number of plants is small, the data in the two crosses in no way conflict. On the contrary, the two crosses act as decided checks upon one another and upon the interpretation assumed to explain modified ratios. Where no modified ratio is expected, that is, where no decided gametic selection has occurred, the duplex 5:1 ratio is approached (table 8). In the reciprocal cross, moreover, a duplex modified ratio of 2:1 is approximated where gametic selection is known to have occurred (table 9).

The plant anthocyan color factor *A* was present in the triploid as either simplex or duplex. Unfortunately one cross ($16_9 \times 56_2$, table 1) made to test this factor produced no kernels. The second cross ($23_8 \times 56_2$, table 1) produced but 9 kernels, 4 colored: 5 colorless. The results merely indicate that the triploid plant was heterozygous for *A*, the numbers being too low to decide between the simplex and the duplex condition.

From what has been stated concerning the inheritance of the factors mentioned above, we are able to reconstruct, to some extent, the constitution of the triploid with regard to these factors as follows: *A?a bbb* $p_1 p_1 p_1$ $T_u T_u t_u$ $s_u s_u s_u$ *Ccc Rrr*.

DISCUSSION

Among investigations on plants several cases of trisomic inheritance have been observed. At present "trisomic inheritance" has two meanings in the literature, both of which, however, depend upon the presence of three instead of two homologous chromosomes.

In the first category the character followed in inheritance depends simply upon the presence of the extra chromosome for its expression. The 2n+1 chromosomal complement produces a particular recognizable character in a plant as contrasted with the 2n condition, and this character may be followed without special reference to the genic constitution of the extra chromosome as compared with that of its homologues. If a 2n+1 individual is crossed on to a 2n individual the phenotypic ratio in F_1 depends solely upon the relative number of individuals which do or do not possess this extra chromosome. Thus, in this type of trisomic inheritance it is the distribution of the extra chromosome that is followed through successive generations.

This kind of inheritance, depending upon an extra chromosome for the expression of a mutant character, has been extensively investigated (BLAKESLEE et al.) in the Datura mutant types Globe (2n+1), Poinsettia (2n+1) etc., each of these types being the result of a duplication of a different chromosome of the set. Other examples are the Nicotiana mutant "enlarged" flower (2n+1) (CLAUSEN and GOODSPEED 1924), the Matthiola mutants Large, Slender, Smooth, Crenate, etc, (FROST and MANN 1924; FROST, 1927), and 2n+1 types in Lycopersicum (LESLEY 1928).

In Zea any one particular chromosome when it is present in triplicate in 2n+1 individuals has not produced, so far as we have noticed, any one particular recognizable character. The presence of extra chromosomes was recognizable, phenotypically, only in decreased size and vigor.

In the second category would come the inheritance of characters which depend upon a factor located in an extra chromosome in a triploid or a 2n+1 individual. It is essentially Mendelian. The ratios obtained in inheritance of the first category are expressions merely of the relative number of 2n and 2n+1 individuals. Those in the second category follow the accepted laws of Mendelian inheritance on a trisomic rather than a disomic basis. In most cases the formulation of an expected ratio would depend upon the assumption of a random assortment at meiosis of the three homologous chromosomes containing the factors in question, and a perfectly random mating. In all cases such expected ratios must be modified by any selective action against certain extra-chromosomal gametic types.

This genic type of trisomic inheritance has been studied in the case of purple and white flower factors in the Poinsettia chromosome of Datura. Recently other gene characters (B-white, swollen, tricarpel) on other chromosomes have been studied (BLAKESLEE 1927; BUCHHOLZ and BLAKESLEE 1927; GAGER and BLAKESLEE 1927). In these cases both types of trisomic inheritance are exhibited together. Trisomic inheritance in Zea, as reported in the present study, is of the second type as indicated by the inheritance of the factors T_u, C and R. LESLEY (1926) has found similar trisomic gene inheritance in tomato.

Among animals the inheritance in chromosomal types other than the diploid has been rather extensively investigated in Drosophila (BRIDGES 1916, 1921, 1922; L. V. MORGAN 1922, 1925; ANDERSON 1925; BRIDGES and ANDERSON 1925).

With regard to Zea it should be kept in mind that the data are necessarily few owing (1) to the limited amount of pollen produced bythe triploid and thus the limited number of crosses that could be made, (2) to the great sterility of this pollen and consequently the few kernels that resulted from each cross, and (3) to the inability to recognize chromosomal types other than by a cytological examination. Hence, the amount of material grown was limited strictly to that which could be studied by one observer in a certain period of time.

SUMMARY

1. A triploid *Zea mays* individual was found in a culture which was otherwise diploid.

2. Meiosis in the microsporocytes of this individual is described. The basic chromosome number in Zea is believed to be ten. At diakinesis and metaphase of the first meiotic mitosis the triploid frequently showed ten trivalents. There was a tendency for members of the extra set of chromosomes to be disassociated from their homologues at diakinesis and metaphase, thus forming nine trivalents, one bivalent and one univalent or eight trivalents, two bivalents and two univalents etc.

3. Reciprocal crosses were made with diploid Zea.

4. Observations on fifty F_1 individuals of the reciprocal crosses of diploid $\times$ triploid were made. It was found that there had been a decided selection against extra chromosome carrying male gametes and a less obvious selection against extra chromosome carrying eggs.

5. The presence of extra chromosomes in Zea plants, other than in a polyploid series, is associated with a decrease in size and vigor.

6. Ratios for several factors (T_u, R and C) were found to accord with the theoretical expectancy on the basis of trisomic inheritance.

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